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Importance of silica solubilising bacteria in agriculture

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Abstract
Essential and non-essential silicate minerals are abundant in soil. In the form of silicic acid, silicon is quickly absorbed by plant roots and transported to active growth regions where it interacts with organic molecules to strengthen cell walls, giving rise to stronger plants. The alteration of insoluble forms of silicate minerals into soluble ones is a crucial function of silicate bacteria. In addition to solubilizing insoluble forms of silicates, potassium and phosphates can also be effectively dissolved by silicate solubilizing bacteria (SSB), which increases soil fertility and boosts plant productivity. By isolating and screening different bacterial strains, it is possible to identify and select the most effective strains that can efficiently solubilize silica in a particular environment or under specific conditions. Since SSB possesses a variety of PGPR traits, it is a superb choice for use as a biofertilizer to promote plant growth. This review is mainly focused on SSB and their role in activities on plants relative to nutritive perspectives, and the potential to utilise this knowledge to supervise a sustainable and environmentally friendly agricultural system.

Keywords: Silica solubilising bacteria, silicon, silicic, PGPR, biofertilizer, sustainable

1. Introduction
In the earth, silicon is mostly found as the silicate mineral sand, quartz (Pure SiO2), kaolinite, mica, fledspar, and other clay minerals (Aluminium, magnesium, calcium, sodium, potassium, or iron). Plants acquire silicon from the soil after it has been depolymerized since it is present there in an unusable polymer form (Epstein, 2009) [14]. Silicon exists as silicic acid (0.1-0.6 mM) in soil solution (Epstein, 2009) [14]. Silica strengthens plant cells which means reduced water loss, less frost damage, more root growth and a decrease in lodging. Silicon fertilizers in agriculture are widespread and they are considered as a modern farm technology with microbiological fertilizers (Bhatti *et al*., 2022) [5]. The alteration of insoluble forms of silicate minerals into soluble ones is a crucial function of silicate bacteria. Additionally, silicate bacteria can dissolve additional plant-friendly elements like potassium. Silicon has positive effect on the biomass yield under deficit irrigation. Silicon shows great influence on the development of plant roots, thus allowing better root resistance in dry soils and its faster growth (Deshmukh *et al*., 2015) [13].
Silicon (Si) improves plant environment relationship as it can improve plants abilities to withstand in adverse climatic conditions due to the presence of natural anti-stress mechanism that empower higher yields and better-quality end products (Marafon and Endres *et al*., 2013) [29]. Si is an agronomically important fertilizer because it enhances plant tolerance capacity to abiotic and biotic stresses (Liang *et al*., 2015) [42]. Si is an abundant element which, when supplied to plants, confers increased vigour and resistance to various stresses, also enhanced stem mechanical strength (Uroz *et al*., 2018) [39]. Si and silica nanoparticles are beneficial for plant growth and protection and can be used as pesticides, herbicides, and fertilizers in agriculture (Garg *et al.*, 2022) [16]. Soil contains a large number of bacteria but only few bacteria found release si from natural silicates, are known as silica solubilizing bacteria (SSB).

2. Silica Solubilizing Bacteria
Silicate solubilizing bacteria (SSB) can play an efficient role not only in solubilizing insoluble forms of silicates but also potassium and phosphates, hence increasing soil fertility and enhancing plant productivity. Silicon benefits the plants in several other ways by accelerating growth, conferring rigidity to leaves thus maximizing leaf surface area for photosynthesis and mitigating the effects of abiotic stresses like drought, salt and metal toxicity in several plants including wheat, rice, sugarcane, cucumber, tomato, citrus and barley (Ma and Yamaji, 2006) [28].

Muralikannan (1996) [30] treatment of SSB with organosiliceous rice straw, husk and husk ash (black char/ash) to rice was found to enhance the growth, chlorophyll content, thousand grain weight, matured grains, biomass and yield. Microorganisms are able to degrade silicates including aluminium silicates. At the time of metabolism in microbes, numerous organic acids are produced and have a twin position in silicate weathering. They supply H^+ ion to the medium make it acidic and promote hydrolysis. Various studies showed the effect of SSB on the nutrient uptake from the soil, their positive effect on photosynthesis and growth of some crops (Han and Lee, 2005; Tripti *et al*., 2017) [18, 38].

The use of SSB in agriculture can have several potential benefits, including improved plant growth, enhanced nutrient uptake, and reduced dependence on chemical fertilizers, enhanced stress tolerance, environmentally friendly approach, and alignment with sustainable agriculture practices. By isolating and screening different bacterial strains, it is possible to identify and select the most effective strains that can efficiently solubilize silica in a particular environment or under specific conditions. This can help ensure that the selected strains are capable of providing the desired benefits in practical applications (More *et al*., 2019) [59]

3. Isolation of silica solubilizing bacteria

Various methods are proposed to solubilize the mineral silica by bacteria and increase its bioavailability for the plants, which includes solubilization due to the production of organic or inorganic acids, alkali, extracellular polysaccharides, or ligands. However, organic acids based solubilization is the most commonly used mechanism by bacteria to dissolve silicate minerals (Cama and Ganor, 2006) [8].

Janardhan *et al*. (2014) [20] isolated four SSB isolates from rhizospheric soils which were collected from wheat, sugarcane, rice and bamboo field of Rahuri, Pune and Solapur. Enrichment media was incorporated with calcium silicate as source of silica. The isolates were tested on graded level of calcium silicate on yield and nutrient uptake in rice.

Naureen *et al*. (2015) [31] isolated total of 111 bacterial strains from various habitats of Pakistan and screened for solubilization of silicate, phosphate and potassium on respective media. Out of these, 35 bacterial isolates were capable of solubilizing either silicate, phosphate or potassium. Amongst these 7 bacterial isolates were capable of solubilizing all three minerals tested. The highest silicate (zone diameter 54 mm) and phosphate solubilization (zone diameter 55 mm) was observed for bacterial isolate NR-2 while the highest potassium solubilization was observed for NE-4b (zone diameter 11 mm).

Sulizah *et al*. (2018) [37] isolated sixteen SSB from paddy rhizosphere which was uprooted from six rice fields, Bangkingan, Jeruk, Kapasan, Sawo, Sumber, Makmur and Siwalan Makmur. and then five of sixteen isolates have a capability to solubilize 0.25% quartz in *Bunt* and *Rovira Agar*.

Shabbir *et al*. (2020) [36] isolated total of 26 from rhizosphere soil of rubber plantation. Based on silicate solubilisation potential, potential SSB with solubilizing activity, plant growth promoting traits and antagonistic activity against *R. microporus*, five bacterial isolates (UPMSSB4, UPMSSB7, UPMSSB8, UPMSSB9 and UPMSSB10) were selected. The isolate UPMSSB7 (*Enterobacter* sp.) had revealed the highest silicate solubilization (11.55 mg L^{-1}), as compared to the other bacterial isolates.

Babu *et al*. (2020) [3] isolated 28 SSB strains from paddy rhizosphere soil samples collected from four districts of Andhra Pradesh. Twenty eight silica solubilizing bacteria (SiSB) isolates were tested for their efficiency by using magnesium trisilicate (0.25%) as an insoluble source of silica in *Bunt* and *Rovira* media.

Different groups have developed the liquid screening media containing different silicon sources *viz*. feldspar, muscovite, biotite, and magnesium trisilicate with soluble phosphate sources (di-potassium hydrogen phosphate; K_2HPO^4 and di-sodium hydrogen phosphate; Na_2HPO^4); and agar based media containing glucose and magnesium trisilicate as sole source of nutrition (Sheng *et al*., 2008; Kang *et al*., 2017; Vasanthi *et al*., 2018) [43, 25, 40]. For the isolation of SSB various media has been used *viz*., Bunt and rovira media (Bunt and rovira, 1955) [7] and silicon solubilizing media (NBRISSM) containing feldspar as silicate (Bist *et al*., 2020).

Insoluble minerals such as silicates, phosphates and potash into soluble form by production of organic acids such as 2 keto- gluconic acid, alkalis and polysaccharides.

Excess production of proton, organic ligands, hydroxyl anion, extra cellular polysaccharides (EPS) and enzymes by SSB leads to the dissolution of silicates.

Sometimes SSB take part in solubilization of other minerals such as potassium and phosphates. Solubilized silicates improve the availability of phosphorus to plants by competing with P fixation sites in soil.Its essentiality for higher plants remains questionable because of the lack of evidence showing Si's direct role in plant metabolism and production of Si-bearing organic compounds (Ma *et al*., 2001; Ma and Takahashi, 2002; Richmond and Sussman, 2003) [44, 46, 47]. Nevertheless, because of the logically flawed definition of essentiality of nutrients (Epstein, 2009) [14], Si being a major inorganic constituent in higher plants, and the significant amount of evidence showing the value of Si in improving crop productivity (Epstein, 1994) [47] Insoluble minerals such as silicates, phosphates and potash into soluble form by production of organic acids such as 2 keto- gluconic acid, alkalis and polysaccharides.

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4. Plant growth promoting attributes

PGPR augments plant growth directly and indirectly but the specific mechanisms involved have all not been well characterized (Glick, 1995) [17]. Eco-friendly approach of utilizing plant-growth-promoting rhizobacteria (PGPR) inoculation and foliar application of silicon (Arruda *et al*., 2013) [2]. Si improves the physiology, growth, and yield of mung bean under saline conditions (Kang *et al*., 2009) [22]. In general, 2-5% of rhizosphere bacteria are PGPR. PGPR can improve plant growth via biological nitrogen fixation, biosynthesis of phytohormones, nutrient solubilization, nutrient uptake, and host plant resistance to biotic and abiotic stresses (Richardson *et al*., 2009; Kang. *et al*., 2014) [35, 23].

4.1 IAA Production

IAA stimulates cell elongation by modifying certain conditions like, increase in osmotic contents of the cell, increase in permeability of water into cell, decrease in wall pressure, an increase in cell wall synthesis and protein synthesis.

Kang *et al*. (2017) [24] found out higher amount of IAA (41.14 ± 10.12 µg mL^{-1}) was produced by CS4-2 grown in high-pH media (pH 8), followed by that produced at pH 7 (8.47 ± 1.02 µg mL^{-1}) and pH 6 (3.6 ± 0.98 µg mL^{-1}) similar findings were made by Chandrakala *et al*. (2019) [9] who discovered that the bacterial isolate produced 0.95-0.14 g of IAA per g of bacterial cell protein.

Cruz *et al.* (2022) [11] found all the 20 SSB isolates as IAA producer in the range of 1.97–77.32 µg mL^{-1}). Isolate Bossier 7 was highest IAA producer (77.32 µg mL^{-1} followed by Newellton-2 86, Alexandria 76 and Vidalia-2113 with 34.21, 33.00, and 32.60 µg mL^{-1}) respectively. Similar results were obtained by Kang *et al*. (2017) [24] highest IAA producer (41.14 ± 10.12 µg mL^{-1}) was CS4-2.

4.2 ACC Deaminase Activity

Microbial ACC-deaminase activity is associated with the biosynthesis and signaling of phytohormone ethylene by preventing the conversion of ACC into ethylene, which enhances the water-holding capacity and alleviates the harmful impact of salinity on roots (Nehela *et al*. 2020) [32]. Al-Garni *et al*. (2019) [1] isolated potential PGPB strains from the rhizosphere soil of alfalfa. All the isolates were screened *in vitro* for their ability to synthesize ACC deaminase. Out of the 25 isolates, ten isolates were able to synthesize. However, only KB-25 displayed the ACC deaminase (0.1 µmol α-ketobutyrate mg^{-1} h^{-1}). These two strains were then tested *in vitro* for their ability to grow and produce ACC deaminase under saline conditions. The results showed that both strains were able to tolerate up to 5% NaCl stress. In addition, we observed no significant changes in the synthesis ACC deaminase by both isolates grown under 5% NaCl stress.

Chandrakala *et al*. (2019) [19] reported the ability of the bacteria to produce 1-aminocyclopropane-1- carboxylate (ACC) deaminase that helps in lowering stress ethylene levels in plants was proven by its capacity to cleave ACC into ammonia and α-ketobutyrate (2.52 ±0.73 µg α ketobutyrate $µg^{-1}$ bacterial cell protein/24 h).

4.3 GA_3 Production

Bagyalakshmi *et al*. (2017) [4] isolated 152 potassium solubilizing bacteria (KSB) from from southern Indian tea plantation soils. Among 152, only thirty were potential for KSB. From thirty only six were found to be efficient potassium solubizing bacteria. The efficiency of all strains were tested for gibberellic acid production.

Panchami *et al.* (2021) [33] screened forty isolate primarily from cardamom rhizosphere, out of twenty six isolates were tested for gibberellic acid production. The highest amount of GA_3 was produced by Wd 6 followed by Pd 1 which produced 36.25 ± 1.05 and 31.50 ± 0.91 µg $mL^{-1}$of GA_3, respectively.

Kubi *et al.* (2021) [26] showed that different bioactive GA_s was observed in the isolate CS51's culture filtrate. The GA_3 was more predominantly detected (38 ± 1.3 ng mL^{-1}) than GA_4 (23 ± 1.2 ng mL^{-1}). Similarly, the isolate CS51 also secretes bioactive GA_3 (21 ± 0.9 ng mL^{-1}) and GA_4 (19 ± 1.0 ng mL^{-1}) under sodium chloride spiked media.

4.4 Siderophore production.

Siderophores promote the growth of plants via iron uptake and subsequent increase of their yield (Vejan *et al*., 2016) [41]. PGPR isolates are also known to release iron-chelating compounds that increase the availability of iron to plants in iron-limiting soils. During this reduction process, the siderophore may be recycled (Rajkumar *et al*., 2010, Neilands, 1995) [34, 49]. Thus, siderophores act as solubilizing agents for iron from minerals or organic compounds under conditions of iron limitation (Indiragandhi *et al*., 2008).

4.5 Ammonia production

Ammonia production is associated with nitrogen fixation in plants that enhance symbiotic association of plant and microorganisms (Jha *et al*., 2015) [21]. Lee *et al.* (2019) [27]

detected ammonia content was found to be higher on GAK2 culture broth (2.90 mg L^{-1}) as compared to control (0.09 mg L^{-1}). Babu *et al.* (2020) [3] shown all the isolates were positive for ammonia production test except SiKPP-5, SiPYY-4 and SiGVV-3 isolates showed the negative.

4.6 Phosphate Solubilisation

Phosphorus availability is enhanced by the uptake of silica which decreases the availability of manganese and iron in plants. Many soil microorganisms are potential solubilizers of bound phosphates. A variety of organic acids such as formic, acetic, propionic, lactic, glycolic, fumaric, and succinic acid are known to reduce the pH of the substrate by secreting phosphate-dissolving bacteria (Subba Rao, 1999) [60]. Many reports on the use of P dissolving bacteria showed increase of plant growth, but some results were not associated to P solubilization. It indicates that other mechanisms were responsible for the positive growth response of plants (Pietr *et al*., 1991; Berthelin *et al*., 1991; De Freitas *et al.*, 1997) [51-53].

Cruz *et al.* (2022) [11] reported nine isolates among 20 SSB to solubilise tricalcium phosphate in pikovskaya's medium showing clearing zone around bacterial colony. Among six SSB isolates where phosphate solubilization index varied from 1.42 to 2.33, maximum phosphate solubilization was exhibited by isolate SSB3 (2.33) by Chopra *et al*. (2021) [10].

4.7 Potassium Solubilization

One of the most vital macro elements for plants is potassium. It is critical for plant growth and plays a significant part in stomatal movement, the creation of various proteins and enzymes, along with ATP and sugar. The lack of it causes plant portions to seem scorched and causes the leaves to yellow. Researchers have created a variety of bio-inoculants to help plants absorb K more effectively because it degrades quickly in soil, which is the only source from which plants can obtain it (Das *et al*., 2016) [12].

Naureen *et al.* (2015) [31] isolated 111 different bacterial strains from different settings in Pakistan and tested for their ability to dissolve potash. The soil samples for NE-4b (zone diameter 11 mm) taken from the Ayubia Mountains had the highest concentration of potash population solubilizers, followed by samples of wheat rhizosphere taken from Narowal, and only a small amount of potash population solubilizers were found in soil samples taken from Rawalpindi.

4.8 Zinc Solubilization

Kumawat *et al*. (2017) [54] correlated zinc levels with zinc-solubilizing potential that are accumulated by plant leaves. The solubilization of zinc phosphate by a strain of *Pseudomonas fluorescence* was reported by Simine *et al.*, (1998) [55]. Chopra *et al*. (2021) [10] reported 4 SSB isolates (SSB3, SSB4, SSB5 and SSB6) out of 6 had shown zinc solublization of 1.5, 1.33, 1.5 and 1.33 respectively

4.9 HCN Production

Hydrogen cyanide is a volatile secondary metabolite that can inhibit the growth of various soil-borne pathogens (Alemu, 2016), due to the inhibition of metal enzymes, especially cytochrome c oxidases in electron transport systems (Siddiqui, 2006) [50]. Ng *et al.* (2016) [61] showed results of HCN production that only four - SSR24, SSR25, SSR26, and SSR27 exhibited positive HCN production, with values ranging from 0.069 to 0.017 of colour density as measured at 625 nm

5. Biochemical characterization

Biochemical test includes *viz.*, starch hydrolysis, citrate utilization, nitrate reduction, gelatine liquefaction, catalase and oxidase.

Sulizah *et al.* (2018) [37] analysed all screened six SSB strains for physiological and biochemical test. All 6 SSB isolates positive for catalase, fermentation of glucose, fructose, sucrose and starch whereas all negative for urease test, 5 positive for citrate utilization, nitrate reduction and indole production test; 4 positive for ornithine, nitrate and citrate test; 3 positive for lactose fermentation, 2 positive for methyl red and fermentation of mannitol and one positive for voges proskauer test. Janardhan *et al*. (2014) [20] reported four SSB isolates as catalase and oxidase positive. Al. Garni *et al.* (2019) [1] obtained biochemical results from the VITEK 2 system showed that theisolates KB-10 and KB-25 were *Pseudomonas pseudoalcali* genes and *P. putida*, and found positive for catalase and oxidase respectively.

Babu *et al*. (2020) [3] reported different biochemical test for isolated 28 SSB *viz.*, starch hydrolysis, hydrogen sulphide test, catalase, oxidase, gelatine liquefaction, indole production, citrate utilization, methyl red, vogesproskauertest. All 28 isolates were positive for starch hydrolysis, hydrogen sulphide test and indole production test. 26 positive for vogesproskauertest, 25 isolates were catalase positive and citrate utilization, 24 were positive for gelatine liquefaction and methyl red test, 21 were oxidase positive,

6. Molecular Characterization

Molecular techniques have assisted to develop easy and rapid process to perform characterization of microbe at genus, species and even at strain-level. ARDRA (Amplified r DNA Restriction Analysis) is the technique of RFLP to gene encoding the small (165) ribosomal unit of bacteria which involves enzymatic amplification using primers at the end of 16S gene. Pattern obtained can be used for phylogenetically characterization of isolates. Repetitive Sequence-based PCR (rep-PCR) techniques, BOX-PCR and ERIC-PCR can be used to evaluate diversity between the native strains and distinguish them efficiently.

ARDRA applied to study microbial diversity is based upon the DNA polymorphism of conserved region 16S rRNA gene. This is a PCR-based technique comprising the principle of restriction fragment length polymorphism (RFLP) of 16S rRNA gene. ARDRA method is widely utilized for the genotyping, variability analysis and community investigations.

ARDRA 16S rRNA gene amplification was performed, and endonuclease digestion analysis of each amplicon was performed separately with Mspl, Hinfl, Haelll, and Alul (Achouak *et al*., 2000) [56]. A dendrogram was formed to determine genetic distance or proximity among the isolated strains (Mehri *et al*., 2011) [57].

Santaro *et al*. (2016) [62] used restriction endonucleases *Alu* I, *Msp* I, *Hinf* I, and *Hae* III because of their ability to discriminate among *Pseudomonas* strains (Achouak *et al.*, 2000; Wu *et al*., 2009; Mehri *et al*., 2011) [56, 58, 57]. For each analyzed strain, a single amplicon (~1400 bp) was obtained using the primers rD1 and fD1. Only seven of the 40 markers gave monomorphic bands. *Alu*I had the highest

polymorphism, generating six different Restriction Fragment Length Polymorphism (RFLP) patterns. *Hinf*I and *Hae* III each generated four RFLP patterns, and *Msp*I generated two RFLP patterns, resulting in less informative restriction. 16S rRNA RFLP patterns obtained using each of the endonucleases were combined to obtain a general genotype for each strain. Genotype 1, the most frequent, was present in 16 native fluorescent strains.

Analysis of *Hae* III generated patterns resulted in the recognition of four different ARDRA patterns, which grouped isolates belonging to the same species together: 20 isolates of *P. plecoglossicida*, 2 isolates of *P. fluorescens*, 2 isolates of *P. libaniensis*, and 1 isolate of *P. aeruginosa*. Therefore, the fingerprints generated by the *Hae*III ARDRA could be used to differentiate isolates belonging to different groups but failed to differentiate those belonging to the same species.

Chandrakala *et al.* (2019) [9], Lee *et al.* (2019) [27], Bisht *et al* (2020) [6], Shabbir *et al.* (2020) [36] and Cruz *et al.* (2022) [11] identified selected silica solubilizing strain by 16S rDNA gene sequence analysis.

7. Conclusion

The review allows us to understand the current situation regarding silica solubilising bacteria. The increasing demand for biofertilizers reflects an eco-friendly and sustainable agriculture system in the future. However, knowledge about soil properties, field environment, and host specificity of strains is mandatory for the successful production and application of biofertilizers. Recent advances in the field of molecular biology, biotechnology, genetic engineering, microbial taxonomy, and nanotechnology have played a significant role in the production of biofertilizers with improved efficiency, higher competitive ability, and multiple functionalities. SSB affect of the rhizoids of the bryophyte *Hypnum plumaeforme* L. in order to determine how it altered the growth and weathering of Si in maize (*Zea mays* L.) (Hu *et al*. 2019) [63]. The concentrations of soluble Si released from the feldspar and quartz powder in liquid media with strain B1-5 inoculation were higher than those of the control. B1-5 inoculation in pot soil significantly increased the water-extractable Si content in soil, improved Si uptake and accumulation in maize plants, and promoted seedling growth. Furthermore, the yield and yield components of different rice cultivars as well as other high-Si-consuming crops such as sugarcane should also be studied.

The recent observations displayed that the use of silica solubilizing bacteria has alleviate different abiotic and biotic stresses and also as PGPR, positively lessened the detrimental impact of co-stressors in addition to enhanced morpho-physiological characteristics and productivity (Etesami *et al*. 2018; Bisht *et al*. 2020) [15, 6]. Biofertilizers can maintain crop productivity with low environmental impact and can be an effective substitute for chemical fertilizers.

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